

## Review Article

# Managing Soil Biota-Mediated Decomposition and Nutrient Mineralization in Sustainable Agroecosystems

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Received 30 June 2014; Revised 13 October 2014; Accepted 17 October 2014; Published 13 November 2014

Academic Editor: Elke Bloem

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Transformation of organic residues into plant-available nutrients occurs through decomposition and mineralization and is mediated by saprophytic microorganisms and fauna. Of particular interest is the recycling of the essential plant elements—N, P, and S—contained in organic residues. If organic residues can supply sufficient nutrients during crop growth, a reduction in fertilizer use is possible. The challenge is synchronizing nutrient release from organic residues with crop nutrient demands throughout the growing season. This paper presents a conceptual model describing the pattern of nutrient release from organic residues in relation to crop nutrient uptake. Next, it explores experimental approaches to measure the physical, chemical, and biological barriers to decomposition and nutrient mineralization. Methods are proposed to determine the rates of decomposition and nutrient release from organic residues. Practically, this information can be used by agricultural producers to determine if plant-available nutrient supply is sufficient to meet crop demands at key growth stages or whether additional fertilizer is needed. Finally, agronomic practices that control the rate of soil biota-mediated decomposition and mineralization, as well as those that facilitate uptake of plant-available nutrients, are identified. Increasing reliance on soil biological activity could benefit crop nutrition and health in sustainable agroecosystems.

## 1. Introduction

Agricultural scientists and practitioners face major challenges in the 21st century. They must produce enough nutritious food to feed a growing world population, which is increasing at rate of 1.14% per year and expected to reach 9.5 billion by 2050 [1]. Agroecosystems are also under pressure to produce greater quantities of fiber for biofuel production. For example, the European Union directive on renewable energy set a target of 10% biofuel, while legislation in the United States will require 20% renewables in fuel by 2022. It is critical that these targets be achieved without compromising food production, which is possible with careful agricultural management. The practices of multiple cropping and using by-products of biofuel production as animal feed resulted in an increase of 19 million ha of net harvested area from 2000 to 2010 in the United States, Brazil, Indonesia, Malaysia, China, Mozambique, South Africa, and 27 European Union member states [2]. By 2010, these countries produced 86 billion L

of ethanol and 15 billion L of biodiesel and also had a net gain in land available to produce food for human and animal consumption [2].

Boosting agricultural production to a level that meets concurrent demands for food and biofuel must be done in a sustainable manner, such that societal objectives and economic prosperity can be achieved without environmental damage. There is concern that agricultural activities have disturbed the natural N and P cycles to the point that they exceed their planetary boundaries [3]. However, initial estimates of the planetary boundaries appear to be low, leading de Vries et al. [4] to revise the N limits after considering N requirements to feed the world's population while avoiding adverse impacts of reactive N in water, air, and soils. Still, sustainable agroecosystems need to be managed to recycle nutrients efficiently, thus reducing reliance on external nutrient and energy inputs. They should also resist abiotic and biotic stresses, allowing them to tolerate periodic disturbances and extreme conditions, such as a short-term

TABLE 1: Attributes of sustainable agroecosystems, based on the ecosystem services concept (adapted from Whalen and Sampedro [17]).

Supporting services	Provisioning services	Regulating services	Cultural services
Sustain energy and material flows Support growth of high-quality agricultural crops Provide habitat for diverse soil fauna	Produce food for people and animals Produce fiber and biofuel Biological products: novel organisms and compounds Generate clean water	Filtration system for percolating water Carbon sequestration and greenhouse gas mitigation Decomposition and nutrient cycling Remediation and attenuation of wastes and pollutants Pest and disease control	Rural communities: past, present, and future Agrotourism Science and education

flooding event or disease outbreak. These attributes also convey resilience so the agroecosystem will continue to be functional and productive if there is a permanent change in the abiotic and biotic stresses that it is subjected to. Adaptive management has a role in supporting agricultural resilience, permitting sustainable agroecosystems to provide ecosystem services to mankind (Table 1).

Soils feature prominently in sustainable agroecosystems because they support tremendous biodiversity that is linked to the health and productivity of crops. Among the millions of species that are permanent soil dwellers include single-celled prokaryotes (Bacteria and Archaea) and eukaryotes (Fungi, Protists, multicellular insects, and annelids). These organisms are sustained by energy inputs from plants, in the form of root exudates and secretions from living plants as well as residues from nonliving plants and other organic wastes. Interactions between plants and soil biota, both symbiotic and free-living inhabitants of the rhizosphere, are emerging as a hot research topic due to the fact that naturally occurring soil biota protect plants against pathogens. For example, vesicular arbuscular mycorrhizal fungi prevent plant diseases through physical and biochemical mechanisms [5], including upregulation of jasmonate induced plant defenses [6, 7]. Systemic resistance, induced by signal molecules released from plant growth promoting rhizobacteria and/or elicitors emitted by nonvirulent pathogens, is also stimulated by auxins released from earthworm activities [8].

Productive crops require nutrients to sustain high yields, and thus plants benefit when soil biota transform organically bound N, P, and S into soluble  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{H}_2\text{PO}_4^-$ ,  $\text{HPO}_4^{2-}$ , and  $\text{SO}_4^{2-}$ , the ionic forms absorbed by root cells. It is known that plants assimilate amino acids, either directly through their roots or via arbuscular mycorrhiza [9], although microorganisms also acquire amino acids from the soil pore water and there is evidence for preferential retention of  $^{15}\text{N}$ -labeled amino acids in soil microbial biomass in low productivity ecosystems (including low input agroecosystems, e.g., [10]). Still, plant N uptake of  $\text{NH}_4^+$ , glutamate-N, and glycine-N was less than 10% of the microbial N uptake from these N forms in a controlled study with *Festuca gigantea* L. under constant soil moisture (60% water-filled pore space) or with wet-dry cycles [11]. In addition, plants bred for high production agroecosystems tend to be less efficient at assimilating organic N forms than  $\text{NH}_4^+$  and  $\text{NO}_3^-$  than their wild relatives [12]. The assumption

in this review is that N mineralization yielding  $\text{NH}_4^+$ , which could be taken up by plants or further transformed via ammonia oxidation and nitrification to produce  $\text{NO}_3^-$ , another plant-available N ion, would be of greater relevance in agroecosystems than uptake of amino acids. Similarly, S mineralization that produces  $\text{SO}_4^{2-}$  was presumed to be of greater importance for plant S nutrition than uptake of the S-containing amino acids, cysteine and methionine [13]. Plants derive nutrition from organic P compounds by secreting extracellular phytases from the root, which facilitates the solubilization and subsequent uptake of  $\text{H}_2\text{PO}_4^-$  [14]. Further information on the contribution of organic N, P, and S to plant nutrition is detailed in the review paper of Paungfoo-Lonhienne et al. [15].

Given that most agricultural crops will assimilate soluble ionic forms of N, P, and S, it is important to understand how all soil biota, from microorganisms to macrofauna, are involved in the decomposition of organic compounds and the mineralization of N, P, and S in the soil-plant system. We can potentially reduce fertilizer inputs if we know how much plant-available N, P, and S will be liberated from organic residues, but will plant-available nutrients be released at the right time during the growing season to satisfy plant nutrient demands? Knowing this will allow us to precisely select the application time and amount of supplemental fertilizers needed to achieve yield goals. Such judicious use of fertilizer is beneficial from an economic perspective, because it will improve nutrient use efficiency, and for the environment since excessive nutrient inputs are susceptible to be transported into waterways and the atmosphere.

Biotic conversion of organically bound nutrients to soluble ions follows a predictable sequence of physical transformations and biochemical reactions, which can be modulated by environmental conditions (e.g., temperature, moisture, and soil physicochemical properties) and agronomic factors (e.g., litter inputs, tillage, and manuring) that affect the activity of the soil biota, as reviewed by Whalen et al. [16]. Fundamentally, it can be viewed as a two-step process that proceeds as follows.

- (1) Decomposition: fragmentation and physical disruption reduces the particle size of the organic residue, which increases the surface area for microbial colonization and hydrolysis by extracellular enzymes. After the chemically complex polymers in the residue

are degraded into monomeric compounds (e.g., amino acids) or ions (e.g.,  $\text{H}_2\text{PO}_4^-$  and  $\text{HPO}_4^{2-}$ ) through these extracellular reactions, they can be absorbed into microbial cells for the second step.

- (2) Mineralization: absorbed monomeric compounds are acted upon by intracellular enzymes, releasing energy and precursors for microbial metabolism (e.g.,  $\text{NH}_4^+$  and  $\text{SO}_4^{2-}$  destined for protein synthesis). Ionic forms of N, P, and S are also absorbed by microbial cells. When microbial requirements are met or when microbial cells are lysed, excess ions can be released into the soil pore water, which is accessible to plant roots.

The purpose of this review is to describe how soil biota mediate the processes of decomposition and nutrient mineralization in sustainable agroecosystems. Next, I discuss how this knowledge can be used to synchronize nutrient release from organic residues and nutrient uptake by agricultural crops, followed by a description of experimental approaches to evaluate the decomposition and nutrient mineralization processes. This approach could permit agricultural managers to increase their reliance on soil biota for nutrient recycling, applying fertilizers strategically to boost the soil nutrient supply at critical growth stages when inherent nutrient reserves are insufficient to meet crop yield goals.

## 2. Decomposition and Nutrient Mineralization: A Two-Step Process

**2.1. Soil Biota Involved in the Decomposition Process.** Organic residue inputs in agroecosystems originate from many sources. Virtually all agroecosystems will have an input of non-harvested crop components—roots, above-ground residues (mostly leaves, stems, and husks) of grain crops, the above-ground biomass of cover crops, green manure crops, and fallow crops—and may also receive organic materials like forestry residues, animal wastes, compost from various feedstocks, and biosolids from municipal water treatment facilities. These wastes are characterized by large particle size and a variable degree of predecomposition at the time they are land applied.

Heterogeneity is the major challenge to describe biologically-mediated decomposition and it arises from a number of factors. First, the variability in physical size, chemical composition, and degree of predecomposition among organic residues makes it difficult to apply them uniformly in agricultural fields. Even if residue from a single crop (e.g., maize) is considered, the amount of organic residue left in the field, its chemical composition, and decomposability is affected by the above-ground and root biomass produced in the previous growing season, the cultivar grown, and genetic modification [22]. Once in the soil, the residue breakdown is mediated by soil organisms that exhibit an aggregated and uneven distribution throughout the soil profile (vertically) and across soil microenvironments (horizontally) [17]. Further, the action of the soil organisms is strongly controlled by oscillations in soil moisture, which is linked to rainfall,

irrigation, and snowmelt patterns as well as evapotranspiration, transpiration, and drainage of water through the soil profile. Wetting-drying cycles are a powerful modulator of soil biota-mediated decomposition and N mineralization [23, 24]. Other important abiotic controls on soil biotic activity are soil texture, soil pH, soil organic matter, and nutrient levels [25, 26]. Variability in these parameters arises during soil pedogenesis and from historical agricultural management. Although small-scale heterogeneity and large-scale gradients that affect the pattern of biologically mediated decomposition and nutrient mineralization need to be considered, this review takes a simplistic view of decomposition and assumes the researcher will account for extraneous, moderator, and mediator variables that produce site-specific conditions affecting decomposition. The conceptual model of decomposition illustrated in Figure 1 is based on senescent crop residue that is left on the soil surface after harvesting a grain crop.

Once a crop reaches physiological maturity, fungi and other microorganisms begin to colonize the senescing leaf and stem tissues of the standing crop, thus initializing the decomposition process before the unharvested residues hit the ground. Still, the senescent crop residues are mostly intact and must be fragmented into smaller particles so that plant cells are physically disrupted and permit microbial and enzymatic access to polymeric compounds. Saprophagous soil macrofauna and mesofauna like earthworms, millipedes, and collembola consume organic residues, which physically fragments the material and mixes it with soil particles containing microorganisms that are ingested by these organisms. For example, pure leaf litter passing through the gut of *Lumbricus terrestris* was reduced in size to  $0.23 \text{ mm}^2$  and further ground to less than  $0.001 \text{ mm}^2$  when sand and litter were consumed together [27]. Litter comminution by earthworms partially or completely buries organic residues, accounting for redistribution of 19 to 24% of the organic matter in crop residues and the top 15 cm of soil each year [28]. These activities result in particle size reduction, which stimulates the soil micro- and mesofauna to further degrade the materials and enhances microbial colonization of the residue. This is supported by the greater abundance and larger biomass of decomposer organisms (bacteria, fungi, protozoa, nematodes, and microarthropods) in buried litter than surface litter [29]. As noted by Beare et al. [29], buried sorghum litter decays more than twice as quickly (1.4–1.7% mass loss per day) as litter left on the soil surface (0.5–0.7% mass loss per day). A similar effect is achieved when residue size is reduced mechanically by tillage in agroecosystems.

After physical barriers to decomposition are overcome by reducing the particle size, the next barrier to decomposition is the chemistry of the polymeric compounds contained in the crop residue. The chemical recalcitrance of plant residues to decomposition and the role of lignin in slowing the decomposition process were reviewed extensively by Gul and Whalen [30] and Gul et al. [31]. Briefly, extracellular enzymes of microbial origin are responsible for cleaving monomeric units from complex polymers like cellulose, hemicellulose,

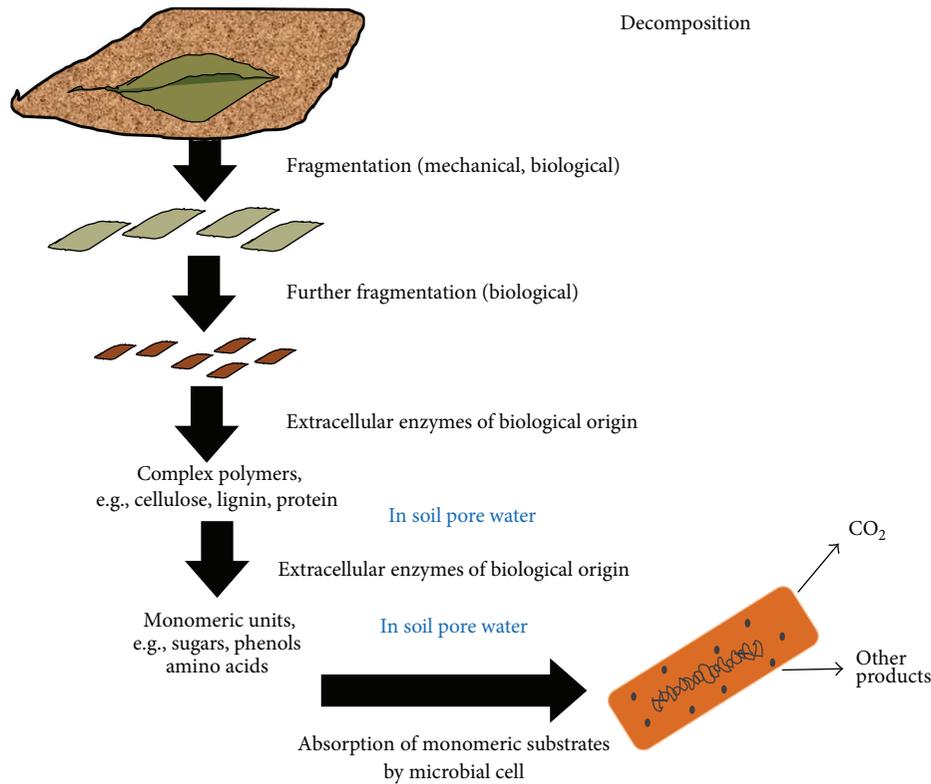


FIGURE 1: Decomposition of senescent crop residue on the soil surface of an agroecosystem. The leaf is fragmented biologically, through the action of soil meso- and macrofauna, and mechanically by tillage or agricultural machinery that passes over the soil surface. Physical fragmentation continues as microorganisms colonize the surface of leaf particles and those particles are ingested by soil fauna. As secondary cell walls are penetrated and cell membranes rupture, complex organic molecules like cellulose, lignin and proteins are released into the soil pore water. Extracellular enzymes produced by microorganisms and plants hydrolyse complex compounds into simple monomeric units like sugars, phenols, and amino acids. Monomeric substrates are then absorbed through the cell membranes of prokaryotes (shown) and eukaryotes (not shown), where they undergo intracellular enzymatic hydrolysis, leading to the production of carbon dioxide (CO<sub>2</sub>) and other metabolic byproducts.

lignin, and proteins. Rates of enzymatic activity are controlled by access to substrates, where access is governed by the amount and chemistry of lignin and lignocellulosic compounds deposited in the secondary cell wall of plants. Water is required for all hydrolytic reactions, which directly affects the functioning of extracellular enzymes as well as the concentration and diffusion of substrates to the active site of the enzyme [32]. For example, low soil moisture (−4 to −1 MPa soil water potential) reduced  $\beta$ -glucosidase activity, such that soils under “drought” had 46% less  $\beta$ -glucosidase activity than those in the ambient moisture treatment in an agricultural field with permanent vegetation [33]. To retain its function, an extracellular enzyme present in soil pore water or attached to a soil organomineral surface must be able to catalyze reactions (i.e., substrates can bind to the active site, the binding affinity of the protein-ligand at the active site is maintained by the tertiary structure, and no inhibitory compounds are bound to the enzyme). Factors affecting extracellular enzyme production and activity include microbial species present, microbial requirements for energy and nutrients that stimulate enzyme production,

temperature, pH, oxygen content, enzyme cofactors, and enzyme inhibitors [34].

Extracellular phosphatases are responsible for mineralizing organic P compounds, all of which are ester phosphates (C–O–P bonds), to soluble, ionic phosphates (predominantly  $\text{H}_2\text{PO}_4^-$  in acidic soils and  $\text{HPO}_4^{2-}$  in alkaline soils) (Figure 2(a)). Similarly, extracellular sulfatases are responsible for the breakdown of ester sulfates (C–O–S bonds) to soluble  $\text{SO}_4^{2-}$  (Figure 2(b)) and extracellular urease converts urea to  $\text{NH}_4^+$  (Figure 2(c)). In the case of plant-derived extracellular phosphatases, the enzyme appears to fulfill two functions: (1) hydrolysis of ester phosphates to  $\text{H}_2\text{PO}_4^-$  or  $\text{HPO}_4^{2-}$  and (2) carrier protein that transports phosphate ions across the plasma membrane [35].

**2.2. Soil Biota Involved in the Mineralization Process.** The decomposition process liberates monomeric compounds that can diffuse through the soil pore water and be absorbed through the membrane of microbial cells for further hydrolysis *in vivo*, releasing energy and precursors for metabolic processes (Figure 3). As described in Whalen et al. [16],

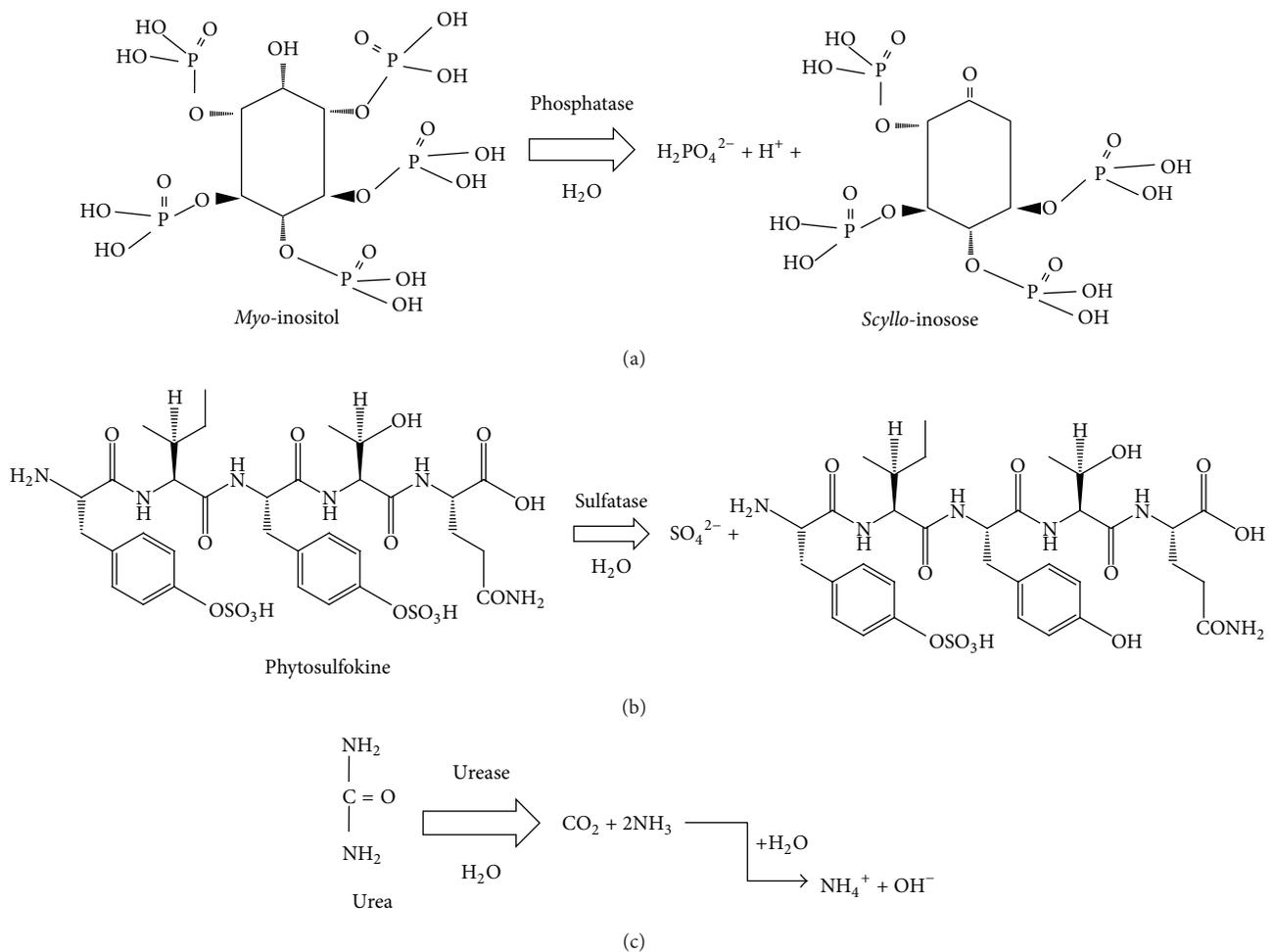


FIGURE 2: Extracellular enzymes are responsible for hydrolysing organic compounds in soil pore water, for example, (a) *myo*-inositol hydrolysis by phosphatase releases  $\text{H}_2\text{PO}_4^{2-}$  and *scyllo*-inosose, (b) phytosulfokine hydrolysis by sulfatase releases  $\text{SO}_4^{2-}$  and a derivative of phytosulfokine, and (c) urea hydrolysis by urease releases carbon dioxide and ammonia, which is converted to  $\text{NH}_4^+$  in the presence of water.

energy-rich compounds like cellobiose are hydrolysed to glucose to fuel reactions in the tricarboxylic acid cycle when oxygen is present, or pyruvate molecules synthesized from glucose are fermented when anaerobic conditions prevail. Amino acids containing N and S C-N and C-S bonds are converted to  $\text{NH}_4^+$  and  $\text{SO}_4^{2-}$  through the action of intracellular amino acid hydrolases. As precursors for protein synthesis and other metabolic pathways, these soluble ions could be immobilized in the microbial cell or released into the soil pore water if microbial requirements were already met. Lysis of microbial cells due to soil disruption (e.g., freezing and thawing, wetting and drying) or grazing by predators (e.g., protists and nematodes) is another way that  $\text{NH}_4^+$  and  $\text{SO}_4^{2-}$  within microbial cells are released into soil pore water.

In aerated soils, the  $\text{NH}_4^+$  produced in the N mineralization process is sequentially oxidized to  $\text{NO}_3^-$  by two groups of organisms, the ammonia oxidizers and nitrifiers (Figure 4). Ammonia oxidizers may be bacteria or archaea that use ammonia monooxygenase to produce  $\text{NH}_2\text{OH}$  and hydroxylamine oxidoreductase to produce  $\text{NO}_2^-$ , in

the process deriving energy for growth from the oxidation of these inorganic compounds and acquiring C from  $\text{CO}_2$  (autotrophic ammonia oxidizers; [36]) or organic C sources (heterotrophic ammonia oxidizers; [37]). Nitrifiers include autotrophic and heterotrophic microorganisms that convert  $\text{NO}_2^-$  to  $\text{NO}_3^-$  with nitrite oxidoreductase [17]. The  $\text{NO}_3^-$  released into soil pore water is readily available to crops due to the high mobility in soil pore water of the  $\text{NO}_3^-$  molecule, relative to  $\text{NH}_4^+$ . However, it is more demanding energetically for plants to use  $\text{NO}_3^-$  for protein synthesis because it has to be first reduced to  $\text{NH}_4^+$  within leaf cells before glutamine production and protein synthesis occur [38].

### 3. Synchronizing the Decomposition and Nutrient Mineralization Processes with Crop Nutrient Requirements

Crops require N to synthesize proteins, chlorophyll, and other N-rich compounds, P for energy relations and cell

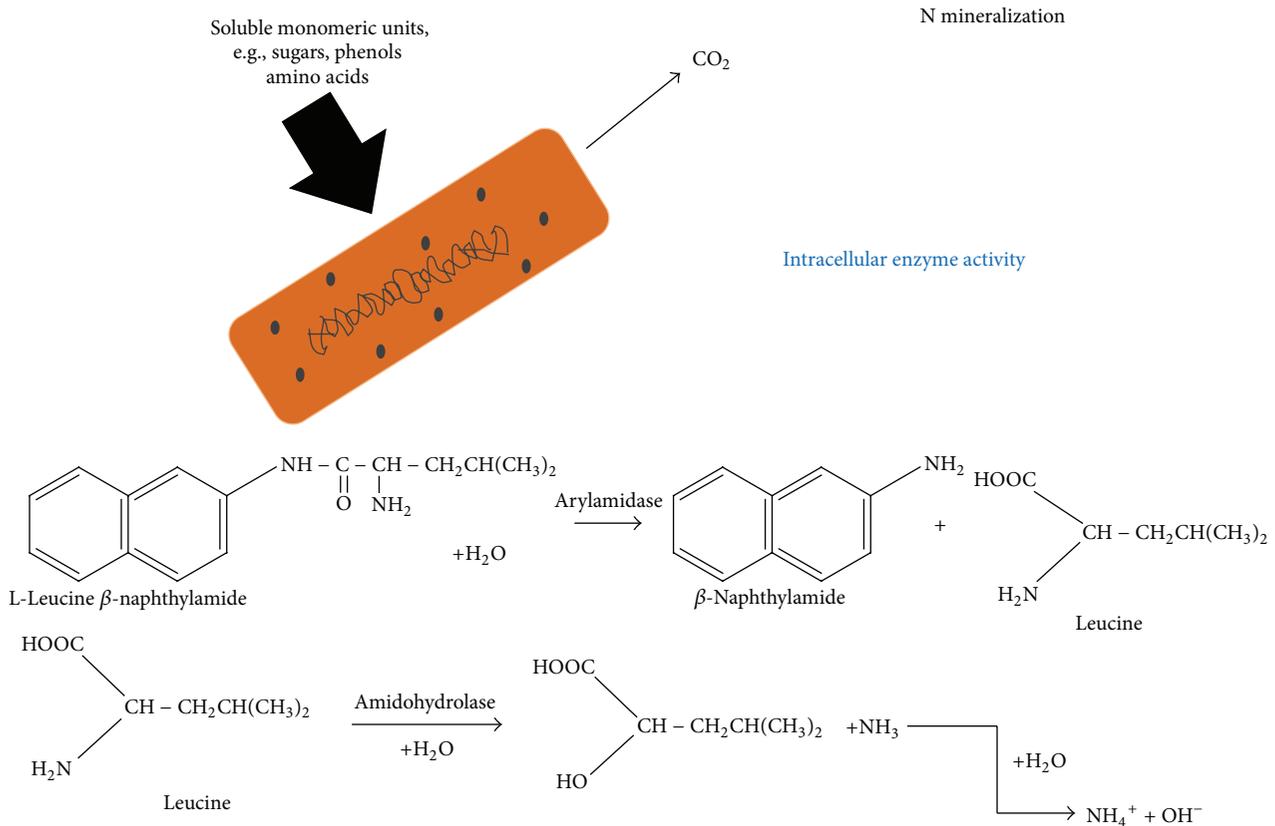


FIGURE 3: Following the absorption of organic N compounds such as amino acids and amino sugars through the cell membrane, intracellular enzymes are responsible for N mineralization, which yields  $\text{NH}_4^+$  as the end product. The  $\text{NH}_4^+$  may be retained in the microbial cell for protein synthesis and other metabolic processes or released from the cell into soil pore water where it can undergo other transformations (e.g., immobilization, plant  $\text{NH}_4^+$  uptake, and  $\text{NH}_4^+$  fixation).

division, and S for protein synthesis, glucosinolate synthesis as an anti-herbivore defense, and production of organosulfur compounds that gives food their distinctive odors and flavors. There is a constant but variable requirement for these nutrients during the growing season. Crop nutrient demands can be predicted roughly from the pattern of biomass accumulation, since nutrient uptake is proportional to the plant's photosynthetic activity, especially during the vegetative growth stage (Figure 5). Estimates of nutrient uptake can be further refined by considering root distribution, biomass, and maximum rooting depth [39].

In crops that derive most or all of their N, P, and S requirements from soil, any impediment to acquiring nutrients from soil pore water could lead to nutrient deficiency at the critical growth stage. The limited mobility of  $\text{H}_2\text{PO}_4^-/\text{HPO}_4^{2-}$  and  $\text{NH}_4^+$  arises from the fact that these ions bind readily to exchange sites on soil organo-mineral surfaces; phosphate ions precipitate with Al, Fe, and Ca minerals as well. Although  $\text{NO}_3^-$  and  $\text{SO}_4^{2-}$  are mobile, moving by mass flow to the roots, rainfall or irrigation events could cause these ions to leach below the root zone where they are inaccessible to the crop [17].

Could soil biota-mediated decomposition and mineralization supply ample N, P, and S at critical crop growth stages?

There are two additional questions that we should consider to narrow the scope of investigation. First, what are the N, P, and S requirements of the crop at the critical growth stage? The assumption is that adequate N, P, and S concentrations in the plant at this growth stage are a good indication of the crop's yield potential. Plant tissue analysis coupled with the Diagnosis and Recommendation Integrated System (DRIS; [40]) or compositional nutrient diagnosis (CND; [41]) is helpful in determining the nutritional requirements for high-yielding crops.

Second, is the quantity of N, P, and S in the organic residues sufficient to meet crop requirements? Taking a mass balance approach, the nutrient stock of the residue (e.g., N concentration in  $\text{kg Mg}^{-1} \times$  residue mass in  $\text{Mg}^{-1}$ ) can be compared to the nutrient removal by the crop (e.g., N concentration in  $\text{kg Mg}^{-1} \times$  crop biomass in  $\text{Mg}^{-1}$ ). However, what proportion of N, P, and S released from the decomposition and mineralization processes is assimilated by the crop at the critical growth stage? We realize that plant-available N, P, and S are subject to microbially mediated reactions (e.g., immobilization, denitrification), chemical adsorption and precipitation reactions, and physical transport in the soil profile, all of which diminish their solubility and accessibility for plant uptake. If the question is asked for a particular crop,

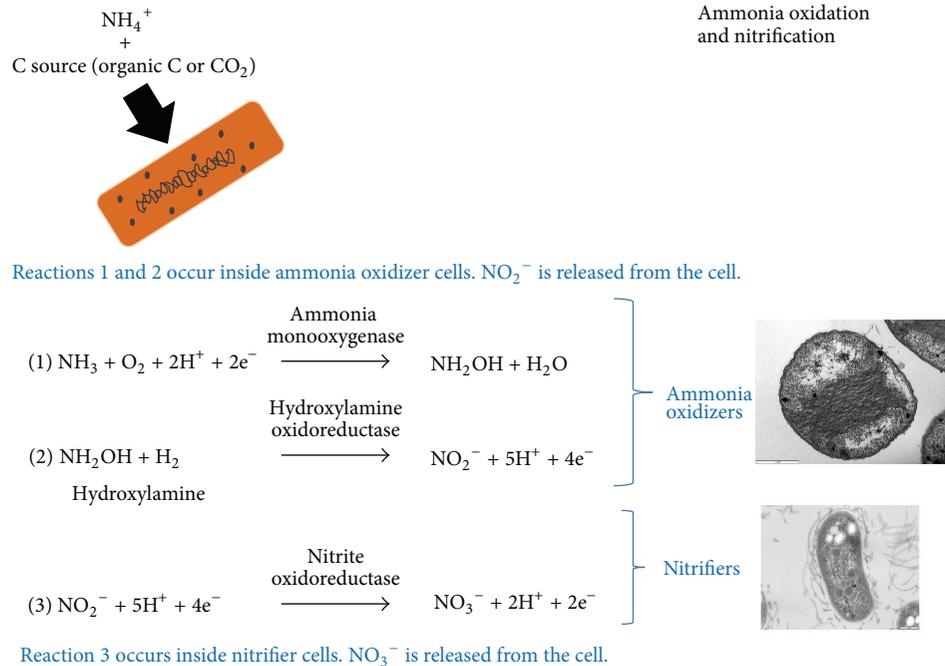


FIGURE 4: Ammonia oxidizers absorb  $\text{NH}_4^+$  from soil pore water and convert it to hydroxylamine and nitrite. Ammonia oxidizers release nitrate into soil pore water, where it is then absorbed by nitrifiers, who convert it to nitrate. Once released into soil pore water, nitrate can undergo other transformations (e.g., immobilization, plant  $\text{NO}_3^-$  uptake, leaching, and denitrification). Top image: transmission electron micrograph of *Nitrosococcus oceani* ATCC 19707 (Klotz et al. [18], copyright American Society of Microbiology). Bottom image: transmission electron micrograph of *Nitrobacter winogradskyi* Nb-255 (Starkenburger et al. [19], image by W. J. Hickey, University of Wisconsin-Madison).

organic residue, and soil type, it could be studied with isotopic tracers ( $^{15}\text{N}$  stable isotopes,  $^{32}\text{P}$ ,  $^{33}\text{P}$ , and  $^{35}\text{S}$  radioisotopes), but the major limitation is that the experiment needs to be repeated for each crop, organic residue, and soil type of interest. Also, the radioisotope work cannot be done in the field for safety reasons, since the relatively short half-life of these radioisotopes (half-life of  $^{32}\text{P} = 14.29$  d;  $^{33}\text{P} = 25.3$  d;  $^{35}\text{S} = 87.2$  d) means that large amounts are needed to monitor P and S transformation rates. Alternative approaches are needed to quantify how soil biota-mediated decomposition and mineralization could contribute to crop nutrition.

#### 4. Experimental Approaches to Evaluate Soil Biota-Mediated Decomposition and Mineralization

Many physical, chemical, and biological tests exist that describe, to some extent, the process of soil biota-mediated decomposition and mineralization. Field-based litterbag studies provide information on the mass loss from organic residues and net release of N, P, and S into soil pore water [42]. Laboratory-based incubation studies under controlled conditions predict the mineralization rate and quantity of soluble N, P, and S generated in soil that was historically or recently amended with organic residues [43, 44]. Biological assays that consider both extracellular and intracellular enzyme activity provide insight into the capacity of the microbial community to hydrolyze organic polymers in soil

pore water and within their cells [34, 45]. While each test method is useful, none can fully describe the processes that transform organic residue into soluble, plant-available nutrients. Experimental approaches are needed that consider (1) the physical barriers to decomposition based on particle size, (2) the chemical barriers to decomposition based on residue chemistry, and (3) the biological barriers to mineralization, arising from biochemical capacity of extracellular and intracellular enzymes, which are strongly controlled by soil temperature and moisture conditions. A conceptual model of the physical, chemical, and biological barriers to soil biota-mediated decomposition and mineralization are illustrated in Figure 6, and methods proposed to evaluate them are listed in Table 2.

#### 5. Agroecosystem Management to Promote Soil Biota-Mediated Decomposition and Mineralization for the Benefit of Crops

Understanding the physical, chemical, and biological barriers to decomposition and nutrient mineralization allows agricultural managers to implement practices that will facilitate soil biological activity. Three control points (Figure 7) are envisioned in this process: (1) control the substrate quantity and quality by selecting appropriate organic residue(s), (2) control the transformation from substrate to product, based on knowledge of the susceptibility of residue to physical breakdown and enzymatic hydrolysis, and (3) control the

TABLE 2: Methods proposed to assess physical, chemical, and biological barriers to soil biota-mediated decomposition and nutrient mineralization.

Physical methods	Chemical methods (in whole soil or soil extracts, for example, hot water extractable organic matter)	Biological methods
Mass loss (litterbags) Light fraction of organic matter Particulate organic matter (whole soil) Particulate organic matter (associated with aggregate size fractions)	<i>Qualitative/semiquantitative</i> Near infrared spectroscopy Fourier-transform infrared spectroscopy Nuclear magnetic resonance spectroscopy (solid-state and soil pore water)	Extracellular enzyme assays (cellobiohydrolase, peroxidase, phenol oxidase, laccase, protease, phosphatase, sulfatase, etc.) Soil respiration ( $\text{CO}_2$ ) Net N, P, and S mineralization Intracellular enzyme assays (dehydrogenase, $\beta$ -glucosidase) Concentrations of soluble $\text{NH}_4^+$ , $\text{NO}_3^-$ , $\text{H}_2\text{PO}_4^-$ , $\text{HPO}_4^{2-}$ , and $\text{SO}_4^{2-}$ ions in soil Concentrations of N, P, and S in plants at critical growth stages
	<i>Quantitative (in whole soil or soil extracts)</i> Organic C, N, P, and S and elemental ratios Fiber analysis (acid detergent and neutral detergent fibers) Cellulose, lignin, and so forth by pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) Proteins, peptides, and so forth by electrospray ionization-liquid chromatography/mass spectrometry (ESI-LC/MS) Ester phosphates by LC-quadrupole time-of-flight (QTOF)/MS Ester sulfates by matrix-assisted laser desorption-ionization time-of-flight/mass spectrometry (MALDI-TOF/MS)	

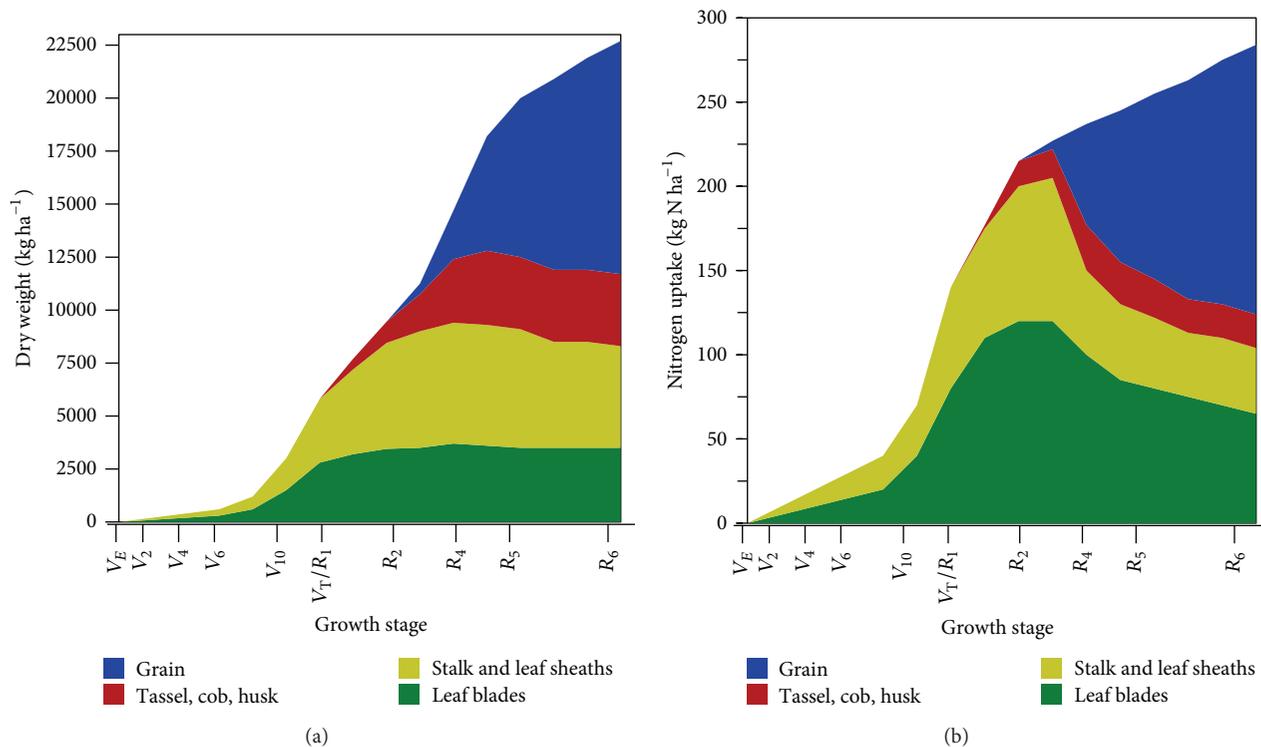


FIGURE 5: Pattern of (a) dry matter accumulation and (b) nitrogen uptake in maize hybrids (modified from [20]). The graphs illustrate the partitioning of dry matter and nitrogen in above-ground components—leaves, stalks, reproductive components, and grain—by growth stages. As described by Abdendroth et al. [21],  $V_E$  refers to vegetative emergence and each subsequent vegetative growth stage is designated  $V_n$  where  $n$  is the number of leaves with visible collar. The  $V_T$  stage indicates tasselling, the final vegetative growth stage when the whole tassel is visible. The subsequent reproductive ( $R_n$ ) growth stages are numbered  $R_1$  (silking, which coincides with pollen shed) to  $R_6$  (physiological maturity).

transfer of product (soluble ions) to the crop. Considering these control points allows agricultural producers to select the right time to apply organic residues, based on expected decomposition and mineralization rates, as well as the crop demand for nutrients during the growing season.

**5.1. Selecting Appropriate Organic Residues.** The quantity of nutrients provided by organic residues is calculated as the total nutrient input of the material, which is appropriate for senescent crop residues and other large, relatively undecomposed materials. When applying partially decomposed

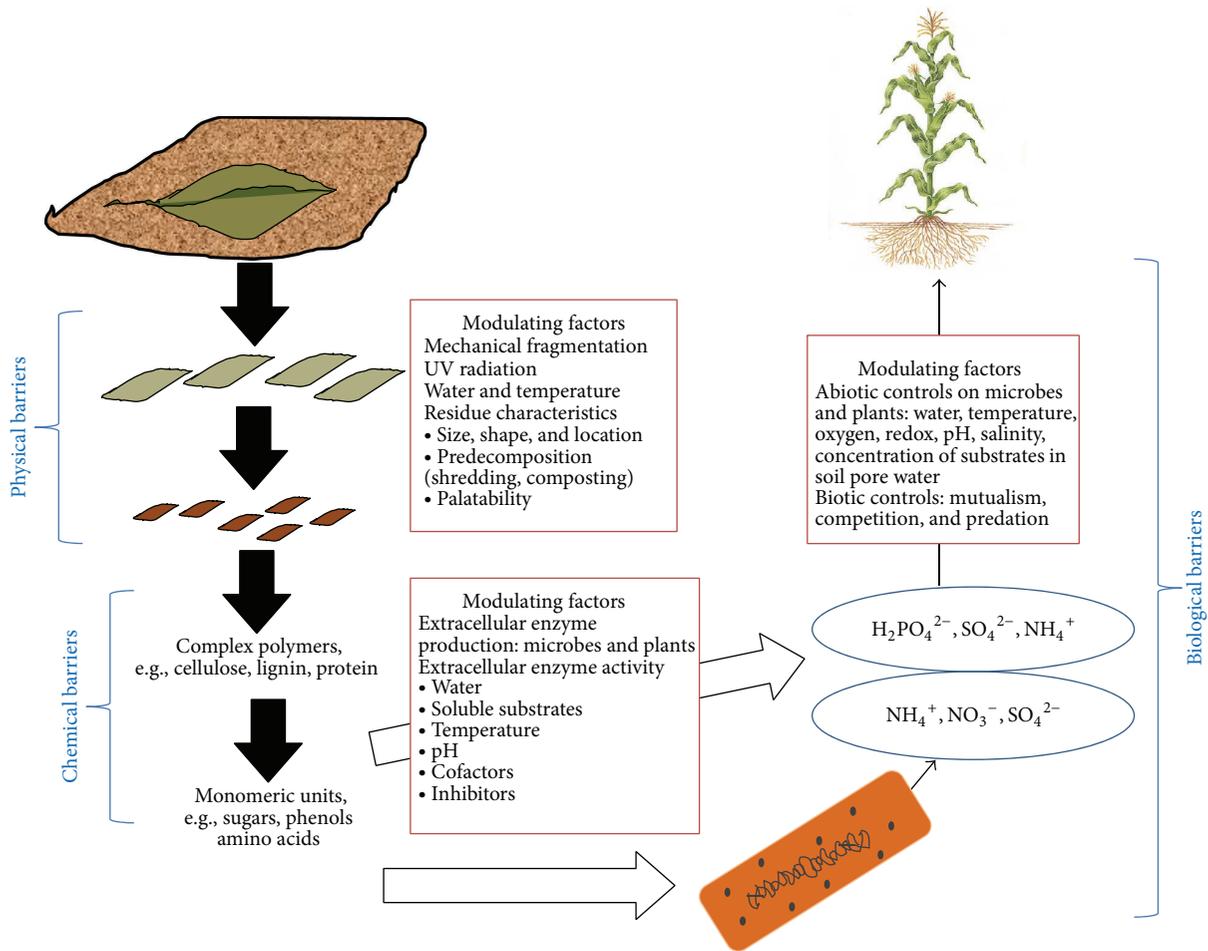


FIGURE 6: Conceptual model of the physical, chemical, and biological barriers to soil biota-mediated decomposition and mineralization. Modulating factors can change the rate at which organic residues pass each barrier and eventually release soluble ions that are taken up by plants.

residues such as compost and animal manure, we must consider the fraction of immediately plant-available nutrients as well. For instance, animal manure contains about 20 to 75%  $NH_4^+$ , with lower values for solid cattle manure mixed with woodchip bedding and the highest proportion of  $NH_4^+$  in liquid pig manure with 3% solids [46]. The rest is organic N, some of which will be decomposed and mineralized during the application year, and the remainder becomes plant-available in a future growing season. In Quebec, Canada, it is estimated that 65 to 90% of the organic N in manure with C:N ratio < 10 is plant-available in the application year, depending on the soil type, crop, application time, and application method. More variability is expected for manure with a C:N ratio > 10, such that 15 to 75% of the organic N is mineralized within one year of application and the undecomposed fraction contributes to a pool of residual organic N that can be mineralized in subsequent growing seasons [46]. There are short windows of opportunity for agricultural producers to apply organic inputs (senescent crop residues, compost, or animal manure), which also affects the decomposition and mineralization process. For instance,

decomposition of surface-applied organic inputs begins after they are plowed down prior to spring planting of annual crops. Although liquid animal manure could be sidedressed between crop rows, either on the soil surface or injected, or broadcast onto forage fields after hay harvesting, there is only a short period in the growing season when this is possible. Producers are aware that heavy agricultural machinery can harm the crop and cause compaction when driven over wet soils and are sensitive to these potential impacts when deciding on when to apply organic residues and how much.

The quality of organic residues is generally described with simple indicators like the C:N ratio and lignin content, often determined by fiber analysis [30]. The chemistry of organic residues is a function of the crop species, the environment in which it is grown, and the agronomic practices followed when it is added to the agroecosystem. For example, if the organic residues are from a green manure crop, the residue quality will be impacted by the crop species in the green manure ( $N_2$ -fixing crops typically have a lower C:N ratio than nonleguminous crops), the nutrient content of the green manure residues, and the age of the green manure at

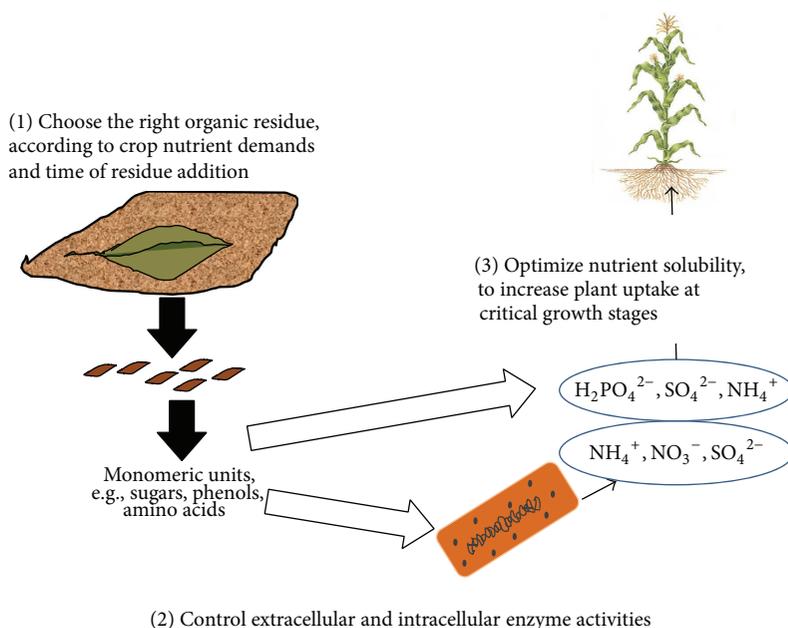


FIGURE 7: Control points where agricultural managers can implement practices to facilitate soil biological activity, leading to nutrient release from organic residues and improving nutrient uptake by crops.

termination, since this controls the residue size and fiber content, including lignin concentration and the C:N ratio [47].

**5.2. Moderating the Organic Residue Decomposition and Mineralization Rates.** As illustrated in Figure 6, soil biota are involved at every step of the decomposition and mineralization process, although their activities can be enhanced or reduced by agronomic practices. For instance, litter fragmentation and comminution are mediated by earthworms and other soil meso- and macrofauna when soil moisture and temperature are appropriate for their activities. Earthworms process appreciable quantities of organic residues (2 to 17  $\text{Mg ha}^{-1} \text{y}^{-1}$  in temperate agroecosystems; [28]), mostly during the spring and autumn months when soils are sufficiently moist and the temperature is typically less than 20°C, which is favorable for earthworms. Although tillage operations can effectively perform the same function as earthworms, increasing the tillage intensity is generally damaging to earthworm populations [48] and energetically costly, so there must be a trade-off between relying on soil biota and tillage to physically reduce organic residues.

Exposure to light and ultraviolet (UV) radiation contributes to organic residue decomposition. Photooxidation by UV-B light (302 nm) increased the solubility of soil organic matter, leading to enhanced oxidation of lignin derived phenols and photochemical degradation of macromolecular soil organic matter species [49]. While biodegradation was the dominant process in litter decomposition, photooxidation and UV radiation altered litter chemistry and destabilized soil organic matter, rendering it more susceptible to decomposition. In semiarid Patagonian steppe ecosystem, Austin and Vivanco [50] concluded that photodegradation had

a dominant control of above-ground litter decomposition. If this phenomenon is important in agroecosystems, exposing senescent organic residues to sunlight for some time, before they are either incorporated by tillage or left on the soil surface in a no-tillage system, would facilitate their decomposition.

Finally, agronomic practices that support a large, diverse microbial community are expected to boost production of extracellular enzymes, which are essential for removing chemical barriers to decomposition. These practices include (1) regular application of organic residues with complex chemistry to support a metabolically diverse microbial community, (2) adding organic residues that are partially decomposed, such as compost and animal manure, to stimulate production of extracellular and intracellular enzymes by soil microorganisms, (3) maintaining vegetative cover to provide energy, in the form of root exudates, to free-living and symbiotic microorganisms that produce extracellular enzymes, and (4) maintaining vegetative cover, to stimulate enzyme release from plant roots [34].

Agricultural practices that modulate soil moisture content could also be important to optimize the activity of hydrolytic extracellular enzymes, as well as those that function intracellularly (e.g., within the cells of ammonia oxidizers and nitrifiers). A target of 60% water-filled pore space would be selected to maximize decomposition by aerobic soil microorganisms [51]. These practices include (1) irrigation, (2) installation of tile drainage lines to remove excess water from fields, particularly in clayey soils that tend to water-logging, (3) retaining mulch and other residues at the soil surface, to improve water infiltration and slow transpiration, and (4) synchronizing organic residue incorporation with rainfall, based on the amount and intensity of the antecedent

and future rainfall events. Global changes in weather (precipitation amount, frequency, temperature, and extreme weather events) make it ever more important to consider how to manage water for agriculture, since all biological activities leading to nutrient mineralization in relation to crop nutrient demands depend on the soil water status.

**5.3. Improving Uptake of Soluble Ions by the Crop.** The final control point involves getting soluble nutrients to the plant, and the management strategy will depend on nutrient mobility in the soil pore water. Mobile  $\text{NO}_3^-$  and  $\text{SO}_4^{2-}$  ions are transported to the rhizosphere by mass flow, meaning that an extensive root zone and evapotranspiration will facilitate their uptake. Immobile  $\text{NH}_4^+$  and  $\text{H}_2\text{PO}_4^-/\text{HPO}_4^{2-}$  ions are captured through root interception and diffusion, which requires close contact between the ion and the root surface [17]. A well-developed root system will improve acquisition of nutrients as they are released from organic residues, and this is achieved by avoiding compaction in the crop row. In some cropping systems and soil type, seedbed preparation implies tillage of the entire field, while zone tillage and ridge tillage may be adopted for widely-spaced row crops like corn and soybeans.

For maximum nutrient use efficiency, the root system should be sufficiently large and colonized by mycorrhizae to intercept soluble nutrients [52]. Practically, this implies that agricultural managers should slow the mineralization process during the preplanting period and early vegetative growth stages to avoid nutrient losses and promote mineralization during the exponential vegetative growth and reproductive growth stages, after mycorrhizal colonization has occurred and roots have greater capacity to absorb nutrients from soil pore water. Thus, crop residues that take a long time to decompose should be incorporated weeks to months before planting crops, to avoid early-season N and P deficiencies in the crop that are a result of N and P immobilization by microbial biomass. Early-season S deficiency is less often reported and would also be alleviated by applying S-containing amendments well in advance of periods of appreciable crop S demand. In contrast, well-decomposed residues or those with appreciable  $\text{NH}_4^+$  content like compost and animal manure should be applied during the growing season by side-dressing or top-dressing. Producers opting for in-season application of organic residues should be aware of a possible increase in crop susceptibility to diseases caused by fungal pathogens. While phytosanitation issues should be minimal if organic residues have undergone thermophilic decomposition (e.g., composting), the other risk is that well-nourished plants with scant root colonization by arbuscular mycorrhizal fungi may be susceptible to pathogens, given that mycorrhiza confer protection against plant diseases through physical and biochemical mechanisms [5, 6].

## 6. Conclusions

The concepts presented in this review are aimed at the development of a robust model of the soil biota-mediated decomposition and mineralization of organic residues applied to

agricultural soils. This model will be parameterized and validated with experimental data that describes the physical, chemical, and biological barriers to transforming organically bound nutrients into plant-available N, P, and S. It is necessary to describe how those fundamental reactions are modulated by abiotic conditions, such as soil temperature, moisture/oxygen supply, texture and pH, and biotic factors such as the crop species grown and its nutrient uptake pattern during the growing season. This permits the model to simulate site-specific controls on nutrient transfer from organic residues to plants, allowing agricultural producers to adjust their management practices accordingly. It takes time for soil biota to decompose organic residues and release plant-available nutrients, and there will be periods when the crop cannot obtain sufficient nutrients from soil biological activity. This is when supplemental mineral fertilizer will be most effective in boosting crop production, although the amount applied should match the crop needs during those periods and account for the fact that nutrients will be released from organic residues later during the growing season. Careful management of nutrients from all available sources, as described here, is consistent with the goals of sustainable agriculture.

## Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

## Acknowledgments

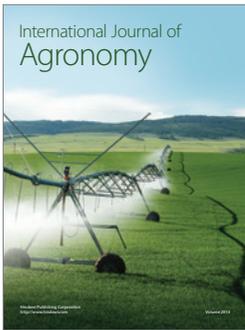
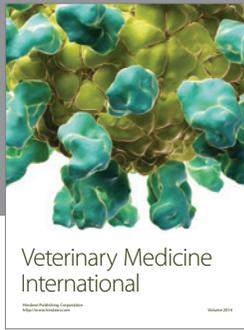
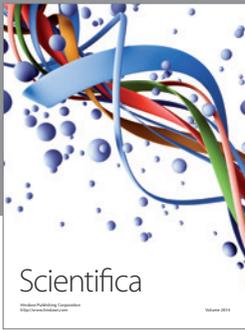
The author thanks the students in Soil Ecology Research Group for helpful discussions and two anonymous reviewers for their insightful critiques of an earlier version of this paper. This work was supported by Grant no. 2383823-10 from the Natural Sciences and Engineering Research Council of Canada (NSERC).

## References

- [1] United Nations, *Population, Development and the Environment 2013*, United Nations, Department of Economic and Social Affairs, Population Divisions, 2013, <http://www.unpopulation.org/>.
- [2] J. W. A. Langeveld, J. Dixon, H. van Keulen, and P. M. F. Quist-Wessel, "Analyzing the effect of biofuel expansion on land use in major producing countries: evidence of increased multiple cropping," *Biofuels, Bioproducts and Biorefining*, vol. 8, no. 1, pp. 49–58, 2014.
- [3] J. Rockström, W. Steffen, K. Noone et al., "Planetary boundaries: exploring the safe operating space for humanity," *Ecology and Society*, vol. 14, no. 2, article 32, 2009.
- [4] W. de Vries, J. Kros, C. Kroeze, and S. P. Seitzinger, "Assessing planetary and regional nitrogen boundaries related to food security and adverse environmental impacts," *Current Opinion in Environmental Sustainability*, vol. 5, no. 3-4, pp. 392–402, 2013.
- [5] G. M. Abdel-Fattah, S. A. El-Haddad, E. E. Hafez, and Y. M. Rashad, "Induction of defense responses in common

- bean plants by arbuscular mycorrhizal fungi," *Microbiological Research*, vol. 166, no. 4, pp. 268–281, 2011.
- [6] S. C. Jung, A. Martinez-Medina, J. A. Lopez-Raez, and M. J. Pozo, "Mycorrhiza-induced resistance and priming of plant defenses," *Journal of Chemical Ecology*, vol. 38, no. 6, pp. 651–664, 2012.
  - [7] Y. Y. Song, M. Ye, C. Y. Li et al., "Priming of anti-herbivore defense in tomato by arbuscular mycorrhizal fungus and involvement of the jasmonate pathway," *Journal of Chemical Ecology*, vol. 39, no. 7, pp. 1036–1044, 2013.
  - [8] R. Puga-Freitas, S. Barot, L. Taconnat, J.-P. Renou, and M. Blouin, "Signal molecules mediate the impact of the earthworm *Aporrectodea caliginosa* on growth, development and defence of the plant *Arabidopsis thaliana*," *PLoS ONE*, vol. 7, no. 12, Article ID e49504, 2012.
  - [9] M. D. Whiteside, M. O. Garcia, and K. K. Treseder, "Amino acid uptake in arbuscular mycorrhizal plants," *PLoS ONE*, vol. 7, no. 10, Article ID e47643, 2012.
  - [10] R. D. Bardgett, T. C. Streeter, and R. Bol, "Soil microbes compete effectively with plants for organic-nitrogen inputs to temperate grasslands," *Ecology*, vol. 84, no. 5, pp. 1277–1287, 2003.
  - [11] K. F. Månsson, M. O. Olsson, U. Falkengren-Grerup, and G. Bengtsson, "Soil moisture variations affect short-term plant-microbial competition for ammonium, glycine, and glutamate," *Ecology and Evolution*, vol. 4, no. 7, pp. 1061–1072, 2014.
  - [12] J. R. Reeve, J. L. Smith, L. Carpenter-Boggs, and J. P. Reganold, "Soil-based cycling and differential uptake of amino acids by three species of strawberry (*Fragaria* spp.) plants," *Soil Biology and Biochemistry*, vol. 40, no. 10, pp. 2547–2552, 2008.
  - [13] V. J. Nikiforova, M. Bielecka, B. Gakière et al., "Effect of sulfur availability on the integrity of amino acid biosynthesis in plants," *Amino Acids*, vol. 30, no. 2, pp. 173–183, 2006.
  - [14] A. E. Richardson, P. A. Hadobas, and J. E. Hayes, "Acid phosphomonoesterase and phytase activities of wheat (*Triticum aestivum* L.) roots and utilization of organic phosphorus substrates by seedlings grown in sterile culture," *Plant, Cell & Environment*, vol. 23, no. 4, pp. 397–405, 2000.
  - [15] C. Paungfoo-Lonhienne, J. Visser, T. G. A. Lonhienne, and S. Schmidt, "Past, present and future of organic nutrients," *Plant and Soil*, vol. 359, no. 1–2, pp. 1–18, 2012.
  - [16] J. K. Whalen, M. L. Kernecker, B. W. Thomas, V. Sachdeva, and C. Ngosong, "Soil food web controls on nitrogen mineralization are influenced by agricultural practices in humid temperate climates," *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, vol. 8, no. 23, pp. 1–18, 2013.
  - [17] J. K. Whalen and L. Sampedro, *Soil Ecology and Management*, CABI Publishers, Wallingford, UK, 2010.
  - [18] M. G. Klotz, D. J. Arp, P. S. G. Chain et al., "Complete genome sequence of the marine, chemolithoautotrophic, ammonia-oxidizing bacterium *Nitrosococcus oceani* ATCC 19707," *Applied and Environmental Microbiology*, vol. 72, no. 9, pp. 6299–6315, 2006.
  - [19] S. R. Starkenburg, P. S. G. Chain, L. A. Sayavedra-Soto et al., "The genome sequence of the chemolithoautotrophic nitrite-oxidizing bacterium *Nitrobacter winogradskyi* Nb-255," *Applied and Environmental Microbiology*, vol. 72, no. 3, pp. 2050–2063, 2006.
  - [20] R. R. Bender, J. W. Haegele, M. L. Ruffo, and F. E. Below, "Nutrient uptake, partitioning, and remobilization in modern, transgenic insect-protected maize hybrids," *Agronomy Journal*, vol. 105, no. 1, pp. 161–170, 2010.
  - [21] L. J. Abdendroth, R. W. Elmore, M. J. Boyer, and S. K. Marlay, "Corn growth and development," PMR 1009, Iowa State University Extension, Ames, Iowa, USA, 2011.
  - [22] S. F. Yanni, J. K. Whalen, and B. L. Ma, "Crop residue chemistry, decomposition rates, and CO<sub>2</sub> evolution in Bt and non-Bt corn agroecosystems in North America: a review," *Nutrient Cycling in Agroecosystems*, vol. 87, no. 2, pp. 277–293, 2010.
  - [23] F. C. Hoyle and D. V. Murphy, "Influence of organic residues and soil incorporation on temporal measures of microbial biomass and plant available nitrogen," *Plant and Soil*, vol. 347, no. 1–2, pp. 53–64, 2011.
  - [24] A. E. Miller, J. P. Schimel, T. Meixner, J. O. Sickman, and J. M. Melack, "Episodic rewetting enhances carbon and nitrogen release from chaparral soils," *Soil Biology and Biochemistry*, vol. 37, no. 12, pp. 2195–2204, 2005.
  - [25] A. Lamparter, J. Bachmann, M.-O. Goebel, and S. K. Woche, "Carbon mineralization in soil: impact of wetting-drying, aggregation and water repellency," *Geoderma*, vol. 150, no. 3–4, pp. 324–333, 2009.
  - [26] V. Poirier, D. A. Angers, P. Rochette, and J. K. Whalen, "Initial soil organic carbon concentration influences the short-term retention of crop-residue carbon in the fine fraction of a heavy clay soil," *Biology and Fertility of Soils*, vol. 49, no. 5, pp. 527–535, 2013.
  - [27] O. P. Schulmann and A. V. Tiunov, "Leaf litter fragmentation by the earthworm *Lumbricus terrestris* L.," *Pedobiologia*, vol. 43, no. 5, pp. 453–458, 1999.
  - [28] J. K. Whalen and R. W. Parmelee, "Quantification of nitrogen assimilation efficiencies and their use to estimate organic matter consumption by the earthworms *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L.," *Applied Soil Ecology*, vol. 13, no. 3, pp. 199–208, 1999.
  - [29] M. H. Beare, R. W. Parmelee, P. F. Hendrix, W. Cheng, D. C. Coleman, and D. A. Crossley Jr., "Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems," *Ecological Monographs*, vol. 62, no. 4, pp. 569–591, 1992.
  - [30] S. Gul and J. Whalen, "Plant life history and residue chemistry influences emissions of CO<sub>2</sub> and N<sub>2</sub>O from soil—perspectives for genetically modified cell wall mutants," *Critical Reviews in Plant Sciences*, vol. 32, no. 5, pp. 344–368, 2013.
  - [31] S. Gul, S. F. Yanni, and J. K. Whalen, "Lignin controls on soil ecosystem services: implications for biotechnological advances in biofuel crops," in *Lignin: Structural Analysis, Applications in Biomaterials and Ecological Significance*, F. Lu, Ed., pp. 375–416, Nova Science, Hauppauge, NY, USA, 2014.
  - [32] S. Manzoni, S. M. Schaeffer, G. Katul, A. Porporato, and J. P. Schimel, "A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils," *Soil Biology and Biochemistry*, vol. 73, no. 6, pp. 69–83, 2014.
  - [33] J. M. Steinweg, J. S. Dukes, and M. D. Wallenstein, "Modeling the effects of temperature and moisture on soil enzyme activity: linking laboratory assays to continuous field data," *Soil Biology & Biochemistry*, vol. 55, no. 12, pp. 85–92, 2012.
  - [34] R. G. Burns, J. L. DeForest, J. Marxsen et al., "Soil enzymes in a changing environment: current knowledge and future directions," *Soil Biology and Biochemistry*, vol. 58, pp. 216–234, 2013.
  - [35] R. B. Lee, "Phosphate influx and extracellular phosphatase-activity in barley roots and rose cells," *New Phytologist*, vol. 109, no. 2, pp. 141–148, 1988.

- [36] D. J. Arp, "Nitrification," in *eLS*, John Wiley & Sons, Chichester, UK, 2009.
- [37] S. Otte, J. Schalk, J. G. Kuenen, and M. S. M. Jetten, "Hydroxylamine oxidation and subsequent nitrous oxide production by the heterotrophic ammonia oxidizer *Alcaligenes faecalis*," *Applied Microbiology and Biotechnology*, vol. 51, no. 2, pp. 255–261, 1999.
- [38] A. Ali, S. Sivakami, and N. Raghuram, "Effect of nitrate, nitrite, ammonium, glutamate, glutamine and 2-oxoglutarate on the RNA levels and enzyme activities of nitrate reductase and nitrite reductase in rice," *Physiology and Molecular Biology of Plants*, vol. 13, no. 1, pp. 17–25, 2007.
- [39] R. E. McMurtrie, C. M. Iversen, R. C. Dewar et al., "Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging," *Ecology and Evolution*, vol. 2, no. 6, pp. 1235–1250, 2012.
- [40] S. T. Dara, P. E. Fixen, and R. H. Gelderman, "Sufficiency level and diagnosis and recommendation integrated system approaches for evaluating the nitrogen status of corn," *Agronomy Journal*, vol. 84, no. 6, pp. 1006–1010, 1992.
- [41] L. E. Parent, A. N. Cambouris, and A. Muhawenimana, "Multivariate diagnosis of nutrient imbalance in potato crops," *Soil Science Society of America Journal*, vol. 58, no. 5, pp. 1432–1438, 1994.
- [42] J. M. Blair, "Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern appalachians," *Soil Biology and Biochemistry*, vol. 20, no. 5, pp. 693–701, 1988.
- [43] J. K. Whalen, C. Chang, and B. M. Olson, "Nitrogen and phosphorus mineralization potentials of soils receiving repeated annual cattle manure applications," *Biology and Fertility of Soils*, vol. 34, no. 5, pp. 334–341, 2001.
- [44] M. St. Luce, J. K. Whalen, N. Ziadi, and B. J. Zebarth, "Nitrogen dynamics and indices to predict soil nitrogen supply in humid temperate soils," *Advances in Agronomy*, vol. 112, pp. 55–102, 2011.
- [45] B. A. Caldwell, "Enzyme activities as a component of soil biodiversity: A review," *Pedobiologia*, vol. 49, no. 6, pp. 637–644, 2005.
- [46] Centre de Référence en Agriculture et Agroalimentaire du Québec (CRAAQ), *Guide de référence en fertilisation*, Centre de Référence en Agriculture et Agroalimentaire du Québec (CRAAQ), Québec, Canada, 2nd edition, 2010.
- [47] R. Dinesh and R. P. Dubey, "Nitrogen mineralization rates and kinetics in soils freshly amended with green manures," *Journal of Agronomy and Crop Science*, vol. 181, no. 1, pp. 49–53, 1998.
- [48] K. Y. Chan, "An overview of some tillage impacts on earthworm population abundance and diversity—implications for functioning in soils," *Soil and Tillage Research*, vol. 57, no. 4, pp. 179–191, 2000.
- [49] X. Feng, K. M. Hills, A. J. Simpson, J. K. Whalen, and M. J. Simpson, "The role of biodegradation and photo-oxidation in the transformation of terrigenous organic matter," *Organic Geochemistry*, vol. 42, no. 3, pp. 262–274, 2011.
- [50] A. T. Austin and L. Vivanco, "Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation," *Nature*, vol. 442, no. 7102, pp. 555–558, 2006.
- [51] D. M. Linn and J. W. Doran, "Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils," *Soil Science Society of America Journal*, vol. 48, no. 6, pp. 1267–1272, 1984.
- [52] A. Elbon and J. K. Whalen, "Phosphorus supply to vegetable crops from arbuscular mycorrhizal fungi: a review," *Biological Agriculture & Horticulture*, 2014.



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